

Rainfall fluctuations and vegetation patterns in alkali grasslands – using self-organizing maps to visualise vegetation dynamics

Vegetationsmuster und Niederschlagsschwankungen in pannonischen Salzsteppen und Salzwiesen – Visualisierung von Vegetationsdynamik mithilfe selbstorganisierender Karten

Balázs A. Lukács¹, Péter Török^{2, *}, András Kelemen³, Gábor Várbíró¹, Szilvia Radócz², Tamás Miglécz², Béla Tóthmérész³ & Orsolya Valkó³

¹Department of Tisza Research, MTA Centre for Ecological Research, Bem tér 18/C, 4026 Debrecen, Hungary, lukacs.balazs@okologia.mta.hu; varbiro.gabor@okologia.mta.hu;

²Department of Ecology, University of Debrecen, Egyetem tér 1, 4032 Debrecen, Hungary, molinia@gmail.com; radoczszilvia88@gmail.com; tamas.miglecz@gmail.com;

³MTA-DE Biodiversity and Ecosystem Services Research Group, P.O. Box 71, 4010 Debrecen, Hungary, kelemen.andras12@gmail.com; tothmerb@gmail.com; valkoorsi@gmail.com

*Corresponding author

Abstract

Knowledge about the drivers of vegetation dynamics in grasslands is fundamental to select appropriate management for conservation purposes. In this study, we provide a detailed analysis of vegetation dynamics in alkali grasslands, a priority habitat of the Natura 2000 network. We studied vegetation dynamics in five stands of four alkali grassland types in the Hortobágy National Park (eastern Hungary), between 2009 and 2011. We analysed the effect of fluctuations in precipitation on both the overall vegetation composition and on the cover of each species using Self Organizing Map neural networks (SOM). We found that SOM is a promising tool to reveal plant community dynamics. As we analysed species cover and overall vegetation composition separately, we were able to identify the species responsible for particular vegetation changes. Fluctuations in precipitation (a dry season, followed by a wet and an average season) caused quick shifts in plant species composition because of an increasing cover of halophyte forbs, probably because of salinisation. We observed a similar effect of stress from waterlogging in all studied grassland types. The species composition of *Puccinellia* grasslands was the most stable over the three years with varying precipitation. This was important as this grassland type contained many threatened halophyte species. Self-organising maps revealed small-scale vegetation changes and provided a detailed visualisation of short-term vegetation dynamics, thus we suggest that the application of this method is also promising to reveal community dynamics in more species-rich habitat types or landscapes.

Keywords: halophytes, neural network, precipitation changes, salt stress, SOM, water stress

Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

According to climate change scenarios, temperate grassland ecosystems will experience considerable changes in precipitation patterns, which can affect community composition and ecosystem functions through altered soil moisture and waterlogging (WHITE et al. 2012, FRY et al. 2013). Similar to Central-European climate change scenarios, extreme future weather conditions are expected for the Pannonian biogeographical region characterised by fluctuating precipitation, extreme temperatures, frequent droughts and decreasing groundwater-levels (FARAGÓ et al. 2010). Thus, it is an important goal to quantify how plant communities respond to interannual climate variation, particularly as it relates to potential management strategies in the face of climate change.

The study of short-term vegetation shifts driven by altered precipitation is particularly important in ecosystems influenced by the groundwater-level, the soil moisture and soil salt concentration, like salt marshes or Eurasian inland alkali grasslands (DEÁK et al. 2014a, b). Saline ecosystems can be found worldwide; there are around 8.31×10^8 ha saline and sodic soils across the globe (DAJIC-STEVANOVIC et al. 2008). Inland alkali grasslands are expected to react highly sensitively to twenty-first century climate change, due to the resulting alteration of precipitation and groundwater-level. Alkali grasslands form highly dynamic spatial and temporal mosaics and the boundary between different grassland types can shift within a short time in accordance with the changes in abiotic environmental characteristics (TIKU 1975, KRÜGER & PEINEMANN 1996). These spatio-temporal changes in species composition are caused by the changing water regime and uneven patterns of alkali salt content in the soil, and can be the result of either seasonal or annual variation in precipitation (MOLNÁR & BORHIDI 2003).

Inland alkali grasslands have a high conservation importance (ZLINSZKY et al. 2015). They are widespread in the Eurasian steppe zone from Mongolia to Eastern-Europe (MOLNÁR & BORHIDI 2003, TÖRÖK et al. 2012). In Europe, extensively grazed Pannonian alkali grasslands in the Hortobágy are among the best preserved open landscapes in Europe (ELIÁŠ et al. 2012, TÖRÖK et al. 2012, 2014). Due to specific climatic and edaphic conditions, these grassland types harbour a unique flora and fauna typical for the Pannonian biogeographical region, and are included in the Natura 2000 network as “*Pannonic salt steppes and salt marshes* (1530)”.

Studies on inland alkali vegetation mostly deal with alkali wetlands and marshes (BOUZILLÉ et al. 2001, BARETT 2006, ÁLVAREZ-ROGEL et al. 2007, MOFFETT et al. 2010, ROZEMA & SCHAT 2012, DEÁK et al. 2014c, 2015a), and only a few studies have been published about inland alkali grasslands. Little is known about the short-term vegetation dynamics of alkali grasslands in relation to fluctuations in seasonal precipitation, although such information would be vital to select the appropriate management for conservation and restoration purposes.

Analysis of vegetation dynamics is an important issue in designing habitat management strategies. Of the diverse methodologies that can be used to analyse vegetation dynamics, self-organizing maps have been suggested as a promising alternative to traditional multivariate analyses, such as MDS or CCA (GIRAUDEL & LEK 2001). The Kohonen Self-Organizing Map (hereafter abbreviated as SOM) is one of the best known neural networks with unsupervised learning rules, which means that it does not need prior classification of the data. SOM was found to be suitable for analysing complex species patterns, for instance in benthic algal assemblages (RIMET et al. 2004) or phytoplankton assemblages (VÁRBÍRÓ et al. 2007), but this tool has been rarely used in vegetation ecology. It is robust to non-linear relation-

ships between variables and their non-normal distributions and was shown to be effective in visualising the data on plant communities sampled using the ordinal-scale Braun-Blanquet phytosociological method (ADAMCZYK et al. 2013). In heterogeneous and highly dynamic environments such as alkali grasslands, grassland types share many common species and the differences of grassland types partly depend on the frequency of these species (DEÁK et al. 2014b). Thus, it is important to know the aggregation pattern of each species separately among grassland types, which can be best explored with SOMs.

Here, we used SOM to reveal changes in species composition in four alkali grassland types. We specifically studied the response of functional groups (halophyte/non-halophyte, graminoid/forb and annual/perennial) to seasonal fluctuating precipitation. We tested the following hypotheses: (1) Grassland type hypothesis: Changes in species richness and species composition are more pronounced in wet grassland types than in dry ones. Plant species of wet grasslands are particularly sensitive to changes in water availability because of the delicate balance between rainfall, temperature and evapotranspiration that governs their physiology (DAWSON et al. 2003). (2) Halophyte hypothesis: The cover of halophyte species increases and that of non-halophyte species decreases due to the increase in salinity after drought events. Changes in precipitation alter soil moisture and salinity, and the changes in these variables promote halophytes as they are tolerant of stressful conditions.

2. Materials and methods

2.1 Study area and sampling

The study area ‘Nagy-szik’ (47° 35’ N and 20° 30’ E) is part of the Hortobágy National Park, eastern Hungary, which is also part of the Natura 2000 network. Detailed military maps (1856–66) show that the area was covered by seasonal alkali wetlands. During the 20th century a ditch was built through the area, which decreased the water table. The regulation of surface waters caused deficiencies in the surface- and ground-water levels, thus, alkali wetland vegetation was mostly replaced by dry and wet alkali grasslands. The study area is moderately grazed with sheep and Hungarian grey cattle (VALKÓ et al. 2014).

The alkali landscapes in the Hortobágy National Park are characterised by a large number of vegetation types, caused by fine-scale elevation patterns. At the highest elevations, loess grasslands are typical (TÓTH & HÜSE 2014), followed by dry alkali grasslands and open alkali swards (TÖRÖK et al. 2012, DEÁK et al. 2014b). The lowest depressions are characterised by alkali meadows and wetlands (DEÁK et al. 2014a, b, c, 2015a). Recent studies found that alkali vegetation types are positioned along a vertical elevation gradient of only few decimetres (ALEXANDER et al. 2015, DEÁK et al. 2014b, 2015b, VALKÓ et al. 2014).

We studied the vegetation dynamics of the four most widespread grassland types in the study area: (i) ARG: *Artemisia* grasslands (*Artemisia santonici-Festucetum pseudovinae* Soó in Máthé 1933 corr. Borhidi 1996) at the highest elevations; two *Puccinellia* grassland types (*Puccinellietum limosae* Magyar ex Soó 1933) in intermediate positions: (ii) PUG-H were situated at higher and (iii) PUG-L at lower elevations, and (iv) JUG: *Juncus* grasslands (*Agrostio-Caricetum distantis* Rapaics ex Soó 1939) at the lowest elevations. Elevation (a.s.l.) was measured with a TOPCON GRS-1 in the centre of each plot with an accuracy of 1–3 cm (for elevation ranges see Fig. 1). ARG is the driest grassland type, characterised by a stable water regime and moderate salinity. PUG-H and PUG-L are dry grassland types with astatic water regime and high salinity. JUG is a mesic grassland type with astatic water regime and moderate salinity (KELEMEN et al. 2013, VALKÓ et al. 2014). We sampled five stands of each grassland type. In each stand we randomly selected 5 permanent plots of 1 × 1-m size; in total we sampled 25 plots per grassland type per year. The percentage cover of vascular plants was recorded each year from 2009 to 2011 in late June. Species names follow KIRÁLY (2009).

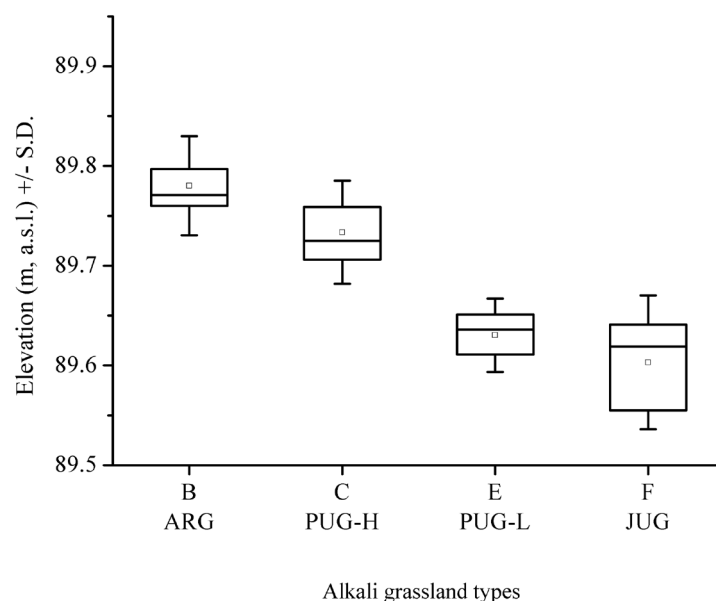


Fig. 1. Mean elevation (m, a.s.l.) of the grassland types. Notations: ARG – *Artemisia* short alkali grasslands; PUG-H – higher elevation *Puccinellia* open alkali grasslands; PUG-L – lower elevation *Puccinellia* open alkali grasslands; JUG – *Juncus* short alkali grasslands. Notations: Boxes indicate 25–75 percentiles, lines are medians, squares are means and whiskers are standard deviations.

Abb. 1. Mittlere Höhe (m ü. NN) der untersuchten Vegetationstypen. ARG – hoch gelegene *Artemisia*-Rasen; PUG-H – höher gelegene *Puccinellia*-Rasen; PUG-L – tiefer gelegene *Puccinellia*-Rasen; JUG – tief gelegene *Juncus*-Rasen. Die Boxen zeigen die 25–75-Perzentile, die Linien den Median, die Quadrate den Mittelwert und die Fehlerbalken die Standardabweichung.

The climate of the region is continental but undergoes large fluctuations in the mean annual temperature and precipitation. The mean annual temperature is 10 °C. The mean annual precipitation of the area is 568 mm (upper quartile 644 mm; lower quartile 476 mm) based on long-term records of the nearest station of the Hungarian Meteorological Services in Debrecen (calculated from January 1901 to December 2000). Figure 2 shows the annual and monthly sum of precipitation and mean temperatures. The first year of the study (precipitation was 402 mm from July 2008 to June 2009) was found to be drier than the climatic average (568 mm); the second was characterised by high precipitation (686 mm from July 2009 to June 2010), while the third was average in terms of precipitation (591 mm from July 2010 to June 2011). Annual and monthly mean temperatures showed no remarkable differences among the three years (mean annual temperature ranged from 10.4 up to 11.3 °C).

2.2 Data analysis

All species were classified as annual/perennial, forb/graminoid and halophyte/non-halophyte. Halophyte categorisation was based on their relative ecological indicator values for salinity (SB; i.e. indicator values of ELLENBERG et al. (1992) modified by BORHIDI (1995) to Hungarian conditions). The range of the SB indicator value scale is from 0 to 9. We considered species having at least SB = 5 value as halophytes. We set up eight functional groups according to life-form categories: annual-graminoid, perennial-graminoid, annual-forb, perennial-forb, halophyte-graminoid, non-halophyte-graminoid, halophyte-forb and non-halophyte-forb. The cover of functional groups, total vegetation cover, total species richness and species richness of the functional groups among years within community types were compared using one-way ANOVA and Tukey tests (ZAR 1999).

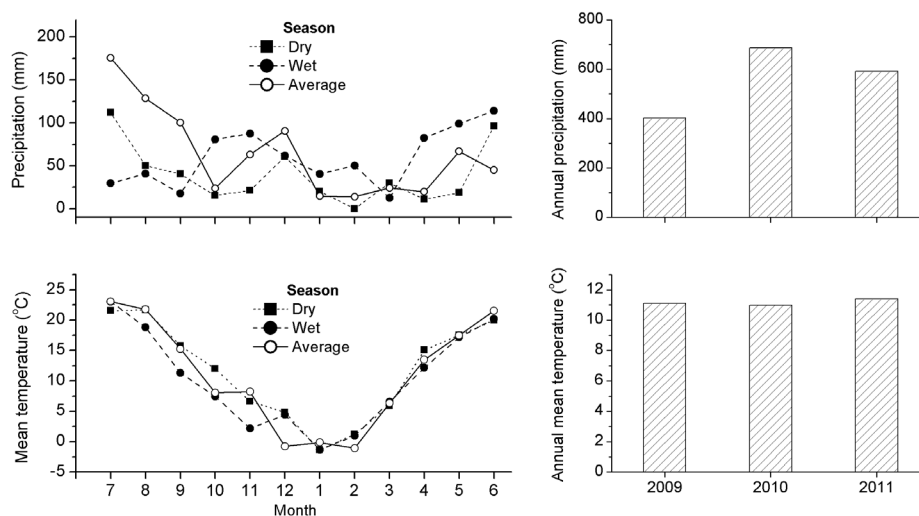


Fig. 2. Monthly and annual precipitation (mm) and mean temperature values (°C) of the Nagy-szik (Hortobágy, Hungary) in the studied years. Data collected in a local meteorological station. Precipitation and temperature data were averaged per growing season and not calendar year. Dry = dry season (July 2008 – June 2009); Wet = wet season (July 2009 – June 2010); Average = average season (July 2010 – June 2011).

Abb. 2. Monatliche und jährliche Niederschlagsmengen und die monatliche Mitteltemperatur in Nagy-szik (Hortobágy, Ungarn) im Untersuchungszeitraum. Die Daten stammen von einer lokalen Klimastation. Die mittleren Niederschlagsmengen und Temperaturen beziehen sich auf Vegetationsperioden und nicht auf Kalenderjahre: Dry = trockene Periode (Juli 2008 bis Juni 2009), Wet = nasse Periode (Juli 2009 bis Juni 2010), Average = durchschnittliche Periode (Juli 2010 bis Juni 2011).

The raw data matrix for the self-organising map (SOM) analysis contained a total of 300 plots and 65 species. SOM was used to analyse plant species cover values and to visualise grassland compositional types separated by years. SOM is a neural network analysis tool to visualise highly multidimensional data by reducing its dimensionality, but still preserving the most important features of the data. Hence, the topological and metric relationships of the original data are preserved (KOHONEN 2001). SOM differs from ordination methods in its greater robustness and the possibility of analysing extremely high sample sizes, even a couple of thousand sample plots.

To explain the variation of ecological datasets, the most commonly used methods are gradient (PCA, CCA) and cluster analyses. However, these are limited by their sensitivity to the nonlinear behaviour of ecological data and the presence of possible outliers in community datasets (CHON et al. 2000, CHON 2011). In order to avoid these problems and deal with the complexity of ecological datasets, the application of artificial neural networks (ANN) has been widely used because they are capable of dealing with problems with nonlinear and complex ecological data, as well as overcoming problems with outliers. The Kohonen self-organizing map (SOM) as an ANN tool is considered to be efficient at visualising distribution patterns and at indicating the relative importance of environmental factors in the organisation and structure of assemblages.

We used the SOM Toolbox (<http://www.cis.hut.fi/projects/somtoolbox>) to implement the SOM in a MATLAB™ environment. Cover values from the three years were analysed separately, whereby each data matrix consisted of 100 samples. Cover values for each species were log normalised before the rescaling process. The map size of the output nodes was chosen according to a heuristic equation $5\sqrt{n}$ of VESANTO & ALHONIEMI (2000). In the selection phase of creating the SOM, the weights of the output layer were initially assigned randomly. Then a sample was chosen randomly and the best match-

ing unit (BMU) was selected by calculating the Euclidean distance between the weights of the input layer and the output layer. Selection of the BMUs was based exclusively on the species cover. When the learning phase was finished, a map with hexagons was obtained in which each hexagon contained a virtual unit containing the calculated weight/species composition. The resulting hexagon map with its weights was visualised using the SOM Toolbox as component planes (CPs). Each CP represents the supplied variables that the SOM algorithm has learned. The detailed algorithm of the SOM can be found in KOHONEN (2001) and LEK & GUEGAN (1999) for ecological applications. Unified distance matrix (U-matrix) representation of the Self-Organizing Map visualises the distances between the virtual units. The distances between the adjacent units are calculated and presented with different tones between the adjacent nodes. A dark tone between the units corresponds to a large distance and thus a gap between the weights values in the input space. A light tone between the neurons signifies that the weight values are close to each other in the input space. Light areas can be thought of as clusters and dark areas as cluster separators. After the training session, the SOM units were clustered into groups based on the dendrogram of a hierarchical cluster analysis using Ward's linkage method (LEGENDRE & LEGENDRE 1998) with Euclidean distance (PARK et al. 2004).

3. Results

3.1 Cover of functional groups

We found that ARG had the highest, while PUG-H and PUG-L had the lowest total vegetation cover in all years (Table 1). In 2011, total vegetation cover in JUG became similar to PUG-H and PUG-L after the average precipitation in the previous 12 months. Total vegetation cover decreased significantly in JUG and PUG-L between 2009 and 2010; and in ARG and JUG between the wet 2010 and 2011. We found that species richness was generally highest for all grassland types in 2009. We found a significant decrease of total species numbers from 2009 to 2010 (Table 2). From 2010 to 2011, species richness increased significantly in the two wet grassland types (PUG-L and JUG; Table 2).

We found that the cover of halophyte forbs was lowest in 2010 in all studied grassland types, but it was only significant in PUG-L grasslands. The cover of non-halophyte forbs was lowest in 2010 in all grassland types except for PUG-H, but this difference was only

Table 1. Total vegetation cover in percent (mean \pm SE) of the alkali grassland types in the studied years. ARG – *Artemisia* short alkali grasslands; PUG-H – higher elevation *Puccinellia* open alkali grasslands; PUG-L – lower elevation *Puccinellia* open alkali grasslands; JUG – *Juncus* short alkali grasslands. Different superscript letters indicate significant differences between years within a grassland type (ANOVA, Tukey test, $p < 0.05$).

Tabelle 1. Gesamtdeckung (Mittelwert \pm Standardfehler) in den untersuchten Vegetationstypen im Untersuchungszeitraum. ARG – hoch gelegene *Artemisia*-Rasen; PUG-H – höher gelegene *Puccinellia*-Rasen; PUG-L – tiefer gelegene *Puccinellia*-Rasen; JUG – tief gelegene *Juncus*-Rasen. Unterschiedliche hochgestellte Buchstaben innerhalb eines Vegetationstypen zeigen signifikante Unterschiede zwischen den Jahren an (ANOVA, Tukey-Test, $p < 0,05$).

Grassland type	2009	2010	2011
ARG	88.6 \pm 1.5 ^a	84.9 \pm 1.6 ^a	71.8 \pm 3.9 ^b
PUG-H	56.8 \pm 2.9 ^a	47.2 \pm 4.2 ^{ab}	43.3 \pm 2.6 ^b
PUG-L	59.9 \pm 3.2 ^a	35.8 \pm 4.4 ^b	34.4 \pm 2.4 ^b
JUG	97.1 \pm 1.4 ^a	63.7 \pm 4.7 ^b	48.5 \pm 4.7 ^c

Table 2. Species number (mean \pm SE) of the alkali grassland types in the studied years. ARG – *Artemisia* short alkali grasslands; PUG-H – higher elevation *Puccinellia* open alkali grasslands; PUG-L – lower elevation *Puccinellia* open alkali grasslands; JUG – *Juncus* short alkali grasslands. Different superscript letters indicate significant differences between years within a grassland type (ANOVA, Tukey test, $p < 0.05$).

Tabelle 2. Artenzahlen (Mittelwert \pm Standardfehler) der untersuchten Vegetationstypen im Untersuchungszeitraum. ARG – hoch gelegene *Artemisia*-Rasen; PUG-H – höher gelegene *Puccinellia*-Rasen; PUG-L – tiefer gelegene *Puccinellia*-Rasen; JUG – tief gelegene *Juncus*-Rasen. Unterschiedliche hochgestellte Buchstaben innerhalb eines Vegetationstypen zeigen signifikante Unterschiede zwischen den Jahren an (ANOVA, Tukey-Test, $p < 0,05$).

Grassland type	2009	2010	2011
ARG	10.9 \pm 0.5 ^a	7.4 \pm 0.4 ^b	8.3 \pm 0.52 ^b
PUG-H	10.4 \pm 0.5 ^a	6.9 \pm 0.5 ^b	8.1 \pm 0.6 ^b
PUG-L	10.4 \pm 0.7 ^a	3.6 \pm 0.3 ^c	7.0 \pm 0.5 ^b
JUG	10.8 \pm 0.5 ^a	3.5 \pm 0.3 ^c	7.1 \pm 0.4 ^b

significant in JUG grasslands (Table 3). We detected a significant decrease from 2009 to 2010 in the cover of halophyte forbs in PUG-L; non-halophyte forbs in JUG; annual forbs in PUG-H and PUG-L and perennial forbs in ARG and JUG. Halophyte forbs had the highest cover in the higher-elevated PUG-H grasslands in 2009, while in 2011 their cover was the highest in the lower-elevated PUG-L grasslands (Table 3).

The cover of halophyte graminoids decreased significantly from 2009 to 2011 in the lowest-elevated grassland types (PUG-L and JUG). In the highest-elevated ARG grasslands, the cover of halophyte graminoids was highest in 2011. The cover of non-halophyte graminoids decreased from the wet year (2010) to the average (2011) year in all grassland types, but significant changes were found only in ARG grasslands. The cover of annual graminoids showed no clear trends except for in JUG grasslands, where their cover decreased significantly from 2009 to 2010 and 2011. The cover of perennial graminoids showed no significant changes between years.

3.2 Changes of species composition – SOM analyses

Plots were clustered according to their species composition similarity using the SOM (Fig. 3). Based on the cover data, four distinct compositional types were identified by the clustering of SOMs, which corresponded to grassland types. We found that the variation in precipitation between sampling years had a marked effect on species composition that can be visualised by the pattern of species SOMs (see Supplement E1–3). The species composition of the four grassland types in the three study years is presented in Supplement E4.

3.2.1 Species composition in 2009 after dry conditions

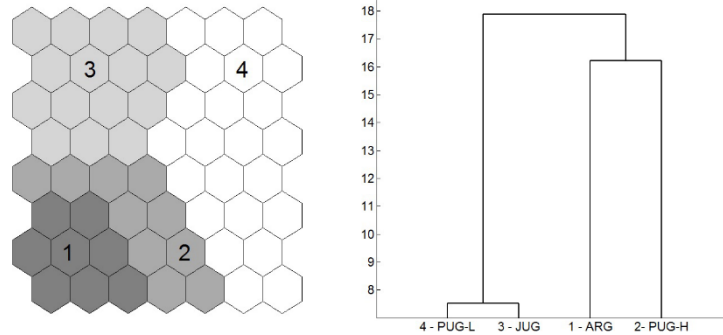
In 2009, the species composition of the four grassland types varied following the elevation gradient. In the cluster diagram, JUG and PUG-L separated into a common branch with small compositional differences (low Ward distance value, Table 4) indicating that the lower elevation grassland types were more similar in species composition. ARG and PUG-H were separated into another branch but had greater differences in their composition (high Ward distance value, Table 3).

Table 3. Cover of functional groups (mean \pm SE) in alkali grassland types in the studied years. Notations: ARG – *Artemisia* short alkali grasslands; PUG-H – higher elevation *Puccinellia* open alkali grasslands; PUG-L – lower elevation *Puccinellia* open alkali grasslands; JUG – *Juncus* short alkali grasslands. Significant differences between years within a grassland type are indicated with different superscript letters and highlighted in bold (ANOVA, Tukey test, $p < 0.05$).

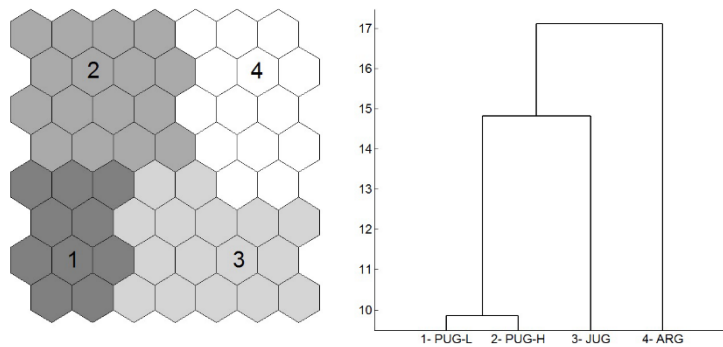
Table 3. Deckungsgrade von funktionellen Artengruppen (Mittelwert \pm Standardfehler) in den untersuchten Vegetationstypen im Untersuchungszeitraum. ARG – hoch gelegene *Artemisia*-Rasen; PUG-H – höher gelegene *Puccinellia*-Rasen; PUG-L – tiefer gelegene *Puccinellia*-Rasen; JUG – tief gelegene *Juncus*-Rasen. Unterschiedliche hochgestellte Buchstaben innerhalb eines Vegetationstypen zeigen signifikante Unterschiede zwischen den Jahren an (ANOVA, Tukey-Test, $p < 0,05$).

	ARG			PUG-H			PUG-L			JUG		
	2009	2010	2011	2009	2010	2011	2009	2010	2011	2009	2010	2011
Halophyte-forb	8.6 \pm 1.0	2.2 \pm 0.5	5.3 \pm 1.1	10.0 \pm 1.5	3.4 \pm 1.7	7.9 \pm 1.2	9.6\pm2.4^b	0.0\pm0.0^c	20.3\pm2.6^a	0.7 \pm 0.3	0.1 \pm 0.1	4.7 \pm 2.6
Halophyte-graminoid	3.5\pm1.0^b	3.1\pm1.0^b	20.2\pm2.7^a	33.4 \pm 2.1	32.2 \pm 7.6	28.7 \pm 1.1	35.4\pm4.0^a	27.2\pm9.5^{ab}	7.5\pm3.4^b	38.2\pm5.5^a	1.5\pm0.7^b	0.6\pm0.2^c
Non-halophyte-forb	4.4 \pm 0.5	1.8 \pm 0.4	3.3 \pm 1.9	6.2 \pm 3.1	0.9 \pm 0.4	0.7 \pm 0.5	6.3 \pm 2.0	0.6 \pm 0.6	2.2 \pm 1.3	7.4\pm1.2^a	0.4\pm0.2^b	4.2\pm0.9^{ab}
Non-halophyte-graminoid	73.3\pm3.6^b	80.0\pm2.1^a	43\pm4.2^c	5.2 \pm 2.3	7.0 \pm 4.8	2.7 \pm 1.6	4.2 \pm 1.6	6.0 \pm 3.2	3.9 \pm 1.9	51.7 \pm 4.9	60.1 \pm 12.3	39.4 \pm 13.6
Annual-forb	3.0 \pm 0.7	1.0 \pm 0.1	5.1 \pm 0.7	12.9\pm2.5^a	2.3\pm1.3^b	7.7\pm1.8^a	13.8\pm2.7^a	0.0\pm0.0^b	21.5\pm2.8^a	3.3 \pm 0.8	0.1 \pm 0.1	5.9 \pm 2.6
Annual-graminoid	3.4 \pm 1.0	1.7 \pm 0.6	12.4 \pm 2.3	18.0 \pm 6.0	7.5 \pm 5.5	3.1 \pm 2.0	17.6 \pm 5.6	26.5 \pm 9.6	0.7 \pm 0.6	36.2\pm4.8^a	1.5\pm0.7^b	0.2\pm0.1^b
Perennial-forb	10.0\pm1.2^a	3.0\pm0.3^b	3.5\pm1.2^b	3.3 \pm 1.1	2.0 \pm 0.9	0.9 \pm 0.7	2.1 \pm 0.7	0.6 \pm 0.6	0.9 \pm 0.7	4.8\pm1.5^a	0.4\pm0.2^b	2.9\pm0.8^{ab}
Perennial-graminoid	73.3 \pm 3.7	81.5 \pm 1.5	50.8 \pm 5.8	20.6 \pm 2.7	31.7 \pm 5.6	28.4 \pm 1.8	22.0 \pm 3.9	6.7 \pm 3.1	10.7 \pm 3.3	53.6 \pm 4.3	60.1 \pm 12.3	39.8 \pm 13.8

2009



2010



2011

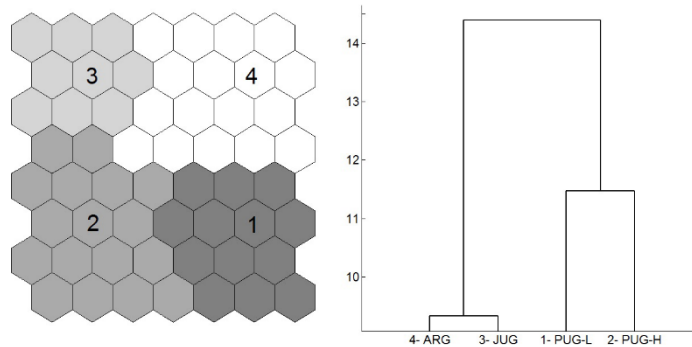


Fig. 3. Visualisation of the distribution patterns of the alkali grassland types in the studied years using self-organizing maps (SOMs) and clusters. The analyses were based on species percentage cover values. Patches in the SOMs refer to cluster branches. Notations: ARG – *Artemisia* short alkali grasslands; JUG – *Juncus* short alkali grasslands; PUG-H – higher elevation *Puccinellia* open alkali grasslands; PUG-L – lower elevation *Puccinellia* open alkali grasslands.

Abb. 3. Mit SOMs und Clusters visualisierte Verteilungsmuster der untersuchten Vegetationstypen. Die Analysen basieren auf prozentualen Deckungswerten der vorkommenden Pflanzenarten. Die SOM-Felder sind komplementär zu den Astlängen der Cluster. ARG – hoch gelegene *Artemisia*-Rasen; PUG-H – höher gelegene *Puccinellia*-Rasen; PUG-L – tiefer gelegene *Puccinellia*-Rasen; JUG – tief gelegene *Juncus*-Rasen.

Table 4. Mean Euclidean distance among alkali grassland types based on relevant SOM clusters (see Fig. 3). Notations: ARG – *Artemisia* short alkali grasslands; PUG-H – higher elevation *Puccinellia* open alkali grasslands; PUG-L – lower elevation *Puccinellia* open alkali grasslands; JUG – *Juncus* short alkali grasslands. Different superscript letters indicate significant differences among years within a grassland type (Tukey test, $p < 0.05$).

Tabelle 4. Mittlere euklidische Distanz aus den SOM-Gruppen zwischen den untersuchten Vegetationstypen (Abb. 3). ARG – hoch gelegene *Artemisia*-Rasen; PUG-H – höher gelegene *Puccinellia*-Rasen; PUG-L – tiefer gelegene *Puccinellia*-Rasen; JUG – tief gelegene *Juncus*-Rasen. Unterschiedliche hochgestellte Buchstaben innerhalb eines Vegetationstypen zeigen signifikante Unterschiede zwischen den Jahren an (ANOVA, Tukey-Test, $p < 0,05$).

Grassland type	2009	2010	2011
ARG	2.24 ^a	1.75 ^b	2.17 ^a
PUG-H	1.53 ^a	1.99 ^b	1.19 ^c
PUG-L	2.24 ^a	1.33 ^b	1.63 ^c
JUG	1.47 ^a	1.14 ^b	1.96 ^c

The similarity of ARG and PUG-H was caused by the high cover of *Artemisia santonicum*, *Trifolium retusum* and *Carex stenophylla* (Supplement E1). ARG was characterised by high cover of *Festuca pseudovina*, *Cynodon dactylon*, *Gypsophila muralis* and *Podospermum canum*. The similarity of JUG and PUG-L was caused by the high cover of *Puccinellia limosa*, *Polygonum aviculare*, *Hordeum hystris*, *Alopecurus geniculatus* and *Cerastium dubium*. PUG-L and PUG-H had a weak separation in the SOM and a clear separation in the cluster diagram. PUG-L had high similarity with JUG, while PUG-H had lower similarity with PUG-L and JUG in the cluster diagram. This separation in the cluster diagram was caused by the different cover values of *Puccinellia limosa*, *Plantago tenuiflora*, *Suaeda maritima*, *Spergularia rubra* and *S. media*.

3.2.2 Species composition in 2010 after wet conditions

The composition of the four grassland types was different in 2010 compared to 2009. In the cluster diagram, PUG-L and PUG-H were separated into a common branch with small compositional differences (low Ward distance value, Table 4, Fig. 3), indicating that *Puccinellia* dominated grassland types became very similar to each other in 2010. JUG and ARG separated from each other and from the PUG types as well (Fig. 3). JUG was found closer to the PUGs while ARG was separated from the other grassland types.

The high similarity of PUG-L and PUG-H was caused by the dominance of *Puccinellia limosa*, *Hordeum hystris* and *Spergularia maritima* in these grassland types. The disappearance or decreased cover of several key species (e.g. *Achillea collina*, *Agropyron repens*, *Agrostis stolonifera*, *Cerastium dubium*, *Suaeda maritima*, *Trifolium* spp.) was the reason for the similarity of JUG, PUG-L and PUG-H (Supplement E2). We detected a significant reduction of species number and total vegetation cover from 2009 to 2010 (Table 1 and 2). The dominance of *Festuca pseudovina* and *Plantago lanceolata* meant that ARG was placed in a separate branch to the other grassland types in 2010. PUG-H and ARG became more different, while PUG-L and PUG-H became more similar to each other after the unusually wet conditions in 2009/2010, compared to the previous year after the dry conditions

(2008/2009). The differentiation of PUG-H from ARG was caused by the decreased cover of *Trifolium angulatum*, *T. retusum*, *Artemisia santonicum* and the dominance of *Puccinellia limosa* in PUG-H.

3.2.3 Species composition in 2011 after average precipitation

After the average season, grassland types were arranged similarly to 2010 but with the difference that JUG and ARG were placed within a common cluster branch with small compositional differences (low Ward distance value, Table 4) indicating that the lowest and the highest elevated grassland types were more similar in species composition to each other than to the PUG grasslands. The increased similarity was caused by the increased cover of *Aster tripolium*, *Hordeum jubatum*, *Cynodon dactylon*, *Taraxacum officinale* and *Trifolium fragiferum* as well as the decreased cover of *Festuca pseudovina* (Supplement E3). The similarity of PUG-L and PUG-H was high in 2010, but it was decreased in 2011. This was caused by the increased cover of *Spergularia media* and *S. rubra*, and the disappearance of *Trifolium angulatum* and *T. retusum* from PUG grasslands.

4. Discussion

Soil salt-content is a key environmental variable in saline ecosystems (WILSON et al. 1996, EALLONARDO et al. 2012), and is directly determined by precipitation (via its effects on groundwater-level) together with temperature (via its effects on evaporation). Therefore, precipitation and temperature are one of the most important factors driving vegetation changes in salt-affected ecosystems (CHENG et al. 2011). Salt-content of the upper soil layer directly depends on the level of groundwater, which is strongly affected by the dynamic relationship between precipitation and evaporation. If groundwater is at an optimal level, summer heat and evaporation will bring water and salts to the upper soil layer. In our study, fluctuating precipitation with constantly high temperatures likely affected soil water- and salt-content, both representing different sources of stress. After the dry year (2009) the water table was likely to be deep below the surface due to severe drought, meaning that the alkali salts remained in the deeper soil layers. The high precipitation in 2010 meant that the groundwater level was raised, so that it covered the surface at lower elevations from June to November. The rising groundwater level in 2010 caused waterlogging stress followed by soil leaching. The amount and distribution of precipitation throughout the year followed the local average in 2010/2011, but the groundwater remained elevated due to the flooding in 2010. This probably led to enhanced salinisation (i.e. the transportation of alkali salts to the soil surface by water) exacerbated by increased evaporation in summer.

We found that the high precipitation in the wet season (2009/2010) favoured graminoids in all grassland types. They retained or increased their cover in all grassland types probably due to their capacity for rapid vegetative growth (KLIMEŠOVÁ & DE BELLO 2009). The increase in cover of *Juncus compressus* and *Agrostis stolonifera* in JUG, *Cynodon dactylon* and *Festuca pseudovina* in ARG, and *Juncus compressus* in PUG-L and PUG-H was responsible for the mean cover increase of graminoids. Nevertheless, graminoids of lower-elevation grasslands, such as *Juncus compressus* especially prefer waterlogged soils and maintain a large seed bank in alkali grasslands (VALKÓ et al. 2014). Thereby, they might be favoured by high water levels in alkali conditions. This also corresponds to the findings of ROZEMA (1975) who found that *Juncus* species were more tolerant to high salinity in flooded than in non-flooded conditions. Moreover, the germination of non-halophyte species was probably

hampered by the long period of water cover in the wet year and also by salt stress in the third year (GRIME 2001). ARG occur at the highest elevation and, hence, were less affected by the increase in the water table and the related salinisation processes than the lower-elevation grassland types (TÖRÖK et al. 2012).

We found that halophyte forbs (e.g. *Artemisia santonicum*, *Podospermum canum* and *Suaeda maritima*) were negatively affected by increased precipitation in the wet year and showed a considerable decrease in their cover values in all grassland types. Several of these species in the study sites were halophytes highly adapted to alkali environments, such as *Spergularia media*, *S. rubra* and *Suaeda maritima*. Seeds of halophytes may be exposed to lower salinity after flooding, thus flooding per se could influence germination (BASKIN & BASKIN 2001). In our study, we found that halophyte forbs did not prefer increased water levels (or even inundation) as indicated by their decreasing cover from 2009 to 2010. Despite their salt-tolerance, their cover increased significantly, probably because of salt stress (from 2010 to 2011) only in PUG-L. This partly contradicted our second hypothesis, because we expected a significant increase in the halophyte forb cover in all grassland types after drought events. Nevertheless, we found that the cover of some halophyte species (especially *Spergularia rubra* and *Suaeda maritima*), which are characteristic species of PUG-H and PUG-L, increased in the other grassland types, thereby causing the shift of PUG-H and PUG-L towards ARG and JUG.

The significant cover increase of halophyte forbs in PUG-L from 2010 to 2011 was likely because water stress was detrimental for almost all species in 2010 in PUG-L. However, they reached their initial cover again in 2011, mainly because of the cover increase of *Spergularia rubra*. This was indicated also by a shift of both PUG-L and PUG-H towards JUG. PUG-L and PUG-H was dominated by *Spergularia rubra* in 2011, while *Crypsis aculeata* and *Atriplex litoralis*, which are characteristic species of PUG-L and PUG-H, appeared only in 2011, likely because of the salt stress. This corresponds to the results of UNGAR (1962, 1991) and BAKKER et al. (1985), who found that *Spergularia* and *Suaeda* species can germinate under higher salt concentrations than other halophytes. MAHMOOD et al. (1996) found that the decrease in soil moisture from 50 to 25% of water holding capacity reduced the germination success of the halophyte species *Suaeda fruticosa* from 40 to 6%. In our study, fluctuating precipitation might have kept soil moisture content at the optimal level for the germination of halophytes. These are important results because *Spergularia media*, *S. rubra* and *Suaeda maritima* are threatened and characteristic species of PUG-H and PUG-L grasslands.

Contrary to our second hypotheses, we found a continuous cover decrease of halophyte graminoids (*Puccinellia limosa*, *Crypsis aculeata* and *Hordeum hystrix*) in the mid- and low-lying grassland types over the studied years. A notable cover increase was found only in ARG grasslands from 2010 to 2011, likely due to salinisation. The general cover decrease was likely triggered by waterlogging stress in 2010. We assume that the vegetative organs of graminoid species were damaged by the long-lasting water cover and could not tolerate the increased salinisation in 2011. On the other hand, high precipitation had a different effect on the non-halophyte graminoids. The cover increase of non-halophyte graminoids in 2010 was mainly caused by the increased cover of *Juncus compressus* and *Agrostis stolonifera* in all grassland types. These species have a much higher tolerance of wet conditions, since these species are characteristic species of wet grasslands.

In 2009, grassland types were arranged according to an elevation gradient confirmed by both the SOM and SOM cluster. In 2010, the extra precipitation caused a remarkable decrease of total vegetation cover in all grassland types, which was most pronounced in the lower-elevation grassland types (JUG and PUG-L; see Table 1). After the extra precipitation during the wet year, the hot and dry summer in 2011 facilitated the accumulation of alkali salts in the upper soil layer. This tendency was also indicated by the position changes of PUG-H and PUG-L grassland types in the cluster branches during the three years.

We found that fluctuating precipitation generally decreased total vegetation cover in all grassland types creating open surfaces for colonisation. This process was more pronounced in the lower elevated JUG, PUG-H and PUG-L grassland types. This confirmed our first hypothesis that changes in species richness and species composition are more pronounced in wet grassland types than in dry ones. This was likely because these grassland types stayed waterlogged for a longer time, which led to the decrease of total vegetation cover. This trend was visualised as the position of JUG, PUG-H and PUG-L changed in the SOM clusters. Another result of precipitation fluctuation was the homogenisation of PUG-L and PUG-H and their increasing differentiation from JUG and ARG. Beside the decrease of total vegetation cover, we found the rearrangement of species composition in PUG, especially the increasing cover of halophytes such as *Puccinellia limosa*, *Suaeda maritima*, *Spergularia media* and *Spergularia rubra*. This result partly confirmed our second hypotheses that changing precipitation and enhanced salinisation promotes halophytes as they are better adapted to changing environments.

5. Conclusions

In our study, SOMs revealed that alkali grassland types respond dynamically to precipitation fluctuations. In the currently changing climate, our findings can provide information for the planning of nature conservation interventions to maintain the highest diversity of grassland types and specialist species. Our results also suggest that in case of such dynamically changing landscapes, species composition of certain grassland types can considerably differ in years with different precipitations. Thus, for a proper habitat assessment of a site, habitat maps and species censuses in dry and wet years should be compared. Self-organising maps are a new, promising tool to analyse complex species patterns, but have so far rarely been used in vegetation ecology. Distance-based methods such as NMDS do not provide species and site scores simultaneously. Like CoA, SOM allows a simultaneous display of the SOM units and of the species but at a much finer scale than CoA. Therefore, the explanation of species scores and the connection of these results to vegetation composition is much better. In our study, self-organising maps revealed small-scale vegetation changes and provided a subtle visualisation of short-term vegetation dynamics in case of species-poor alkali grassland types where many of the species can appear and disappear in any of the studied grassland types according to precipitation alterations. We suggest that the application of this new method is also promising to reveal community dynamics in case of more species-rich habitat types or landscapes.

Erweiterte deutsche Zusammenfassung

Einleitung – Pannonische Salzsteppen und Salzwiesen haben in der Europäischen Union einen hohen Naturschutzwert (TÖRÖK et al. 2012). Der Salzgehalt des Oberbodens dieser Vegetationstypen hängt vom Grundwasserstand ab, welcher wiederum durch den Niederschlag und die Verdunstung bestimmt wird. Zeiträumliche Schwankungen des Salz- und Wassergehaltes des Bodens können zu vorübergehenden (Fluktuationen) aber auch dauerhaften Veränderungen (Sukzessionen) der Vegetation führen (DEÁK et al. 2014a, MOLNÁR & BORHIDI 2003). Pannonische Salzsteppen und Salzwiesen werden als prioritäre Lebensräume in Anhang I der Fauna-Flora-Habitat-Richtlinie aufgeführt, jedoch ist wenig über ihre durch Niederschlagschwankungen bedingte Dynamik bekannt. Solche Kenntnisse können jedoch zum besseren Verständnis dieser Vegetationstypen beitragen und auch zur Planung von Managementmaßnahmen wichtig sein. In dieser Studie stellen wir die Hypothesen auf, dass Niederschlagsschwankungen auf (1) feuchten Salzböden stärkere Veränderungen des Artenreichtums und der Artenzusammensetzung bewirken als auf trockenen Salzböden, und (2) dass bei Versalzung salztolerante Arten in ihrer Abundanz stärker als nicht-salztolerante Arten zunehmen.

Material und Methoden – Im Zeitraum 2009–2011 wurde an fünf Lokalitäten des Hortobágy-National-Parks (Ost-Ungarn) die Vegetationsdynamik von vier Salzsteppen- und Salzwiesentypen nach einer trockenen Periode (Juli 2008 bis 2009), nach einer nassen Periode (Juli 2009 bis 2010) und nach einer hinsichtlich des Niederschlags durchschnittlichen Periode (Juli 2010 bis Juni 2011) untersucht. Pro Lokalität wurden zufällig jeweils fünf 1 × 1 m-Flächen ausgewählt und dauerhaft markiert. Insgesamt untersuchten wir über die drei Jahre pro Vegetationstyp 25 Flächen. Als Vegetationstypen unterschieden wir *Artemisia*-Rasen (ARG; *Artemisia santonici-Festucetum pseudovinae* Soó in Máthé 1933 corr. Borhidi 1996) auf den am höchsten gelegenen Flächen, zwei Typen an *Puccinellia*-Rasen (*Puccinellietum limosae* Magyar ex Soó 1933) auf den mittelhoch gelegenen Flächen – der eine *Puccinellia*-Rasentyp (PUG-H) lag etwas höher und der andere (PUG-L) etwas tiefer – sowie *Juncus*-Rasen (JUG; *Agrostio-Caricetum distantis* Rapaics ex Soó 1939) auf den am tiefsten gelegenen Flächen (Abb. 1).

Die Artenzusammensetzung und deren Veränderung über die Zeit wurden mithilfe sog. selbstorganisierender Karten (SOMs – *self-organising maps*) über die Deckungsgrade der vorkommenden Pflanzenarten visualisiert. SOM ist eine neuronale Netzwerkanalyse zur Visualisierung hochdimensionaler Daten, die in der Lage ist, die Dimensionalität der Daten zu verringern ohne ihre grundsätzliche Struktur zu verändern. SOM ist eine effiziente Methode zur Visualisierung von Verteilungsmustern und des relativen Einflusses von Umweltfaktoren in strukturierten Lebensgemeinschaften.

Ergebnisse – Nach der trockenen Periode war die Artenvielfalt in allen Vegetationstypen am höchsten. Nach der darauffolgenden nassen Periode fiel sie signifikant ab, stieg aber nach der anschließenden, hinsichtlich des Niederschlags durchschnittlichen Periode wieder an. Dieser Anstieg war jedoch nur in den *Juncus*-Rasen und tiefer gelegenen *Puccinellia*-Rasen und damit in den feuchtesten Flächen signifikant und erreichte zudem nicht seinen Anfangswert (Tabelle 2). Nach der nassen Periode war in beiden *Puccinellia*-Rasen die Abundanz der einjährigen Kräuter am niedrigsten, während in den *Artemisia*- und *Juncus*-Rasen jene der mehrjährigen Kräuter am niedrigsten war (Tabelle 3). Die Abundanz der salztoleranten Arten sank über den gesamten Zeitraum in den Vegetationstypen der feuchtesten Standorte (*Juncus*-Rasen und tiefer gelegene *Puccinellia*-Rasen) ab.

Diskussion – Schwankende Regenmengen führen in pannonischen Salzsteppen und Salzwiesen zu teilweise recht schnellen Veränderungen der Vegetation. Innerhalb unserer Studie über drei Jahre mit unterschiedlichen Niederschlägen (nass, trocken, durchschnittlich) konnten wir eine generelle Abnahme der Vegetationsdeckung beobachten, die zur Bildung von offenen (kolonisierbaren) Bodenbereichen führte. Diese Abnahme führen wir vorrangig auf Überstauung der tiefer gelegenen Salzsteppen-/Salzwiesenbereiche und möglicherweise auch auf eine Reduktion des Boden-Salzgehaltes zurück. Diese Vegetationsveränderungen auf kleinräumlicher Skala konnten wir mithilfe von SOMs visualisieren. SOMs wurden in der Vegetationsökologie bislang selten genutzt. Ein Vorteil von SOMs ist die

gleichzeitige Verwendung von Art- und Lebensraumdaten. SOMs stellen ein hervorragendes Instrument zur Analyse und Darstellung mehrdimensionaler (komplexer) Daten und damit zur Darstellung und Erklärung von Vegetationsveränderungen dar.

Acknowledgements

We are grateful to S. Boch, T. Becker and two anonymous reviewers for their useful comments on the manuscript. We are grateful to L. Sutcliffe for language corrections. We would like to thank several students and colleagues (Z. Ecsedi, J. Tar, B. Deák and A. Földi) for their assistance in the field and laboratory. The study was supported by the SROP-4.2.2.B-15/1/KONV20150001 project. The authors were supported by the TÁMOP 4.2.1./B-09/1/KONV-2010-0007, TÁMOP-4.2.2_B-10_1-2010-0024 and TÁMOP- 4.2.4.A/2-11-1-2012-0001 projects, and the ‘Sodic lake habitat restoration in the Hortobágy’ project (LIFENAT07/H/000324). The TÁMOP projects are implemented through the New Hungary Development Plan, co-financed by the European Social Fund and the European Regional Development Fund. G.V. was supported during the writing of this paper by the Bolyai János Research Scholarship of the Hungarian Academy of Sciences. The research was supported by Hungarian Research Fund (OTKA PD 100192; OTKA K 104279; OTKA PD 111807) and the Internal Research Grant of the University of Debrecen.

Supplements

Additional supporting information may be found in the online version of this article.

Zusätzliche unterstützende Information ist in der Online-Version dieses Artikels zu finden.

Supplement E1–E3. Visualisations of species distribution patterns according to the cover values in 2009 / 2010 / 2011.

Anhang E1–E3. Darstellung der Verteilung der Arten entsprechend ihrer Deckungswerte im Jahr 2009 / 2010 / 2011.

Supplement E4. Cover values of the species in the four grassland types in three years.

Anhang E4. Deckungsgrade der Arten in den vier Graslandtypen in den drei Jahren.

References

- ADAMCZYK, J.J., KURZAC, M., PARK, Y.-S. & KRUK, A. (2013): Application of a Kohonen’s self-organizing map for evaluation of long-term changes in forest vegetation. – *J. Veg. Sci.* 24: 405–414.
- ALEXANDER, C., DEÁK, B., KANIA, A., MÜCKE, W. & HEILMEIER, H. (2015): Classification of vegetation in an open landscape using full-waveform airborne laserscanner data. – *Int. J. Appl. Earth Obs.* 41: 76–87.
- ÁLVAREZ-ROGEL, J., JIMÉNEZ-CÁRCELESA, F.J., ROCAA, M.J., ORTIZB, R. (2007): Changes in soils and vegetation in a Mediterranean coastal salt marsh impacted by human activities. – *Estuar. Coast. Shelf Sci.* 73: 510–526.
- BAKKER, J.P., DIJKSTRA, M. & RUSSCHEN, P.T. (1985): Dispersal, germination and early establishment of halophytes and glycophytes on a grazed and abandoned salt-marsh gradient. – *New Phytol.* 101: 291–308.
- BARETT, G. (2006): Vegetation communities on the shores of a salt lake in semi-arid Western Australia. – *J. Arid Envir.* 67: 77–89.
- BASKIN, C.C. & BASKIN, J.M. (2001): *Seeds: Ecology, Biogeography and Evolution of Dormancy and Germination.* – Academic Press, London: 666 pp.
- BORHIDI, A. (1995): Social behaviour types, the naturalness and relative ecological indicator values of the higher plants in the Hungarian flora. – *Acta Bot. Hung.* 39: 97–181.

- BOUZILLÉ, J.-B., KERNEIS, E., BONIS, A. & TOUZARD, B. (2001): Vegetation and ecological gradients in abandoned salt pans in western France. – *J. Veg. Sci.* 12: 269–278.
- CHENG, Y., TSUBO, M., ITO, T.Y., NISHIHARA, E., SHINODA, M. (2011): Impact of rainfall variability and grazing pressure on plant diversity in Mongolian grasslands. – *J. Arid Envir.* 75: 471–476.
- CHON, T.S. (2011): Self-organizing maps applied to ecological sciences. – *Ecol. Inform.* 6: 50–61.
- CHON, T.S., PARK, Y.S., PARK, Y.H. (2000): Determining temporal pattern of community dynamics by using unsupervised learning algorithms. – *Ecol. Model.* 132: 151–166.
- DAJIC-STEVANOVIC, Z., PECINAR, I., KRESOVIC, M., VRBNICANIN, S. & TOMOVIC, L. (2008): Biodiversity, utilization and management of grasslands of salt affected soils in Serbia. – *Community Ecol.* 9: 107–114.
- DAWSON, T.P., BERRY, P.M. & KAMPA, E. (2003): Climate change impacts on freshwater wetland habitats. – *J. Nat. Conserv.* 11: 25–30.
- DEÁK, B., VALKÓ, O., ALEXANDER, C., MÜCKE, W., KANIA, A., TAMÁS, J. & HEILMEIER, H. (2014b): Fine-scale vertical position as an indicator of vegetation in alkali grasslands – case study based on remotely sensed data. – *Flora* 209: 693–697.
- DEÁK, B., VALKÓ, O., TÖRÖK, P., KELEMEN, A., MIGLÉCZ, T., SZABÓ, S., SZABÓ, G. & TÓTHMÉRÉSZ, B. (2015b): Micro-topographic heterogeneity increases plant diversity in old stages of restored grasslands. – *Basic Appl. Ecol.* 16: 291–299.
- DEÁK, B., VALKÓ, O., TÖRÖK, P., KELEMEN, A., TÓTH, K., MIGLÉCZ, T. & TÓTHMÉRÉSZ, B. (2015a): Reed cut, habitat diversity and productivity in wetlands. – *Ecol. Complex.* 22: 121–125.
- DEÁK, B., VALKÓ, O., TÖRÖK, P. & TÓTHMÉRÉSZ, B. (2014a): Solonetz meadow vegetation (*Beckmannia eruciformis*) in East-Hungary – an alliance driven by moisture and salinity. – *Tuexenia* 34: 187–203.
- DEÁK, B., VALKÓ, O., TÓTHMÉRÉSZ, B. & TÖRÖK, P. (2014c): Alkali marshes of Central-Europe – Ecology, Management and Nature Conservation. – In: SHAO H-B (Ed.) *Salt Marshes: Ecosystem, Vegetation and Restoration Strategies*: 1–11. Nova Science Publishers, Hauppauge.
- EALLONARDO JR., A.S., LEOPOLD, D.J., FRIDLEY, J.D. & STELLA, J.C. (2012): Salinity tolerance and the decoupling of resource axis plant traits. – *J. Veg. Sci.* 25: 365–374.
- ELIÁŠ, P., SOPOTLIEVA, D., DÍTĚ, D., HÁJKOVÁ, P., APOSTOLOVA, I., SENKO, D., MELEČKOVÁ, Z. & HÁJEK, M. (2012): Vegetation diversity of salt-rich grasslands in Southeast Europe. – *Appl. Veg. Sci.* 16: 521–537.
- ELLENBERG, H., WEBER, H.E., DÜLL, R., WIRTH, W., WERNER, W. & PAULISSEN, D. (Eds.) (1992): *Zeigerwerte von Pflanzen in Mitteleuropa* 2. Aufl. – *Scr. Geobot.* 18: 1–262.
- FARAGÓ, T., LÁNG, I. & CSETE, L. (2010): Climate change and Hungary: mitigating the hazard and preparing for the impacts (the VAHAVA report). – MTA, Budapest: 124 pp.
- FRY, E.L., MANNING, P., ALLEN, D.G.P., HURST, A., EVERWAND, G., RIMMLER, M. & POWER, S.A. (2013): Plant functional group composition modifies the effects of precipitation change on grassland ecosystem function. – *PLoS ONE* 8: e57027.
- GIRAUDEL, J. & LEK, S. (2001): A comparison of self-organizing map algorithm and some conventional statistical methods for ecological community ordination. – *Ecol. Model.* 146: 329–339.
- GRIME, J.P. (2001): *Plant Strategies, Vegetation Processes and Ecosystem Properties*. – John Wiley & Sons, Chichester: 456 pp.
- KELEMEN, A., TÖRÖK, P., VALKÓ, O., MIGLÉCZ, T. & TÓTHMÉRÉSZ, B. (2013): Mechanisms shaping plant biomass and species richness: plant strategies and litter effect in alkali and loess grasslands. – *J. Veg. Sci.* 24: 1195–1203.
- KIRÁLY, G. (Ed.) (2009): *Új magyar fűvészkönyv. Magyarország hajtásos növényei. Határozókulcsok* (The Vascular Plants of Hungary. Identification key) [in Hungarian]. – Aggteleki Nemzeti Park Igazgatóság, Jósvalfő: 616 pp.
- KLIMEŠOVÁ, J. & DE BELLO, F. (2009): CLO-PLA: the database of clonal and bud bank traits of Central European flora. – *J. Veg. Sci.* 20: 511–516.
- KOHONEN, T. (2001): *Self-organizing maps*. – Springer, Berlin: 502 pp.
- KRÜGER, H.R. & PEINEMANN, N. (1996): Coastal plain halophytes and their relation to soil ionic composition. – *Vegetatio* 122: 143–150.
- LEGENDRE, P. & LEGENDRE, L. (1998): *Numerical Ecology*. – Elsevier, Amsterdam: 852 pp.
- LEK, S. & GUÉGAN, J. (1999): Artificial neural networks as a tool in ecological modelling, an introduction. – *Ecol. Model.* 120: 65–73.

- MAHMOOD, K., MALIK, K.A., LODHI, M.A.K. & SHEIKH, K.H. (1996): Seed germination and salinity tolerance in plant species growing on saline wastelands. – *Biol. Plant.* 38: 309–315.
- MOFFETT, K.B., ROBINSON, D.A. & GORELICK, S.M. (2010): Relationship of salt marsh vegetation zonation to spatial patterns in soil moisture, salinity, and topography. – *Ecosystems* 13: 1287–1302.
- MOLNÁR, Z. & BORHIDI, A. (2003): Hungarian alkali vegetation: Origins, landscape history, syntaxonomy, conservation. – *Phytocoenologia* 33: 377–408.
- PARK, Y.-S., CHON, T.-S., KWAK, I.-S. & LEK, S. (2004): Hierarchical community classification and assessment of aquatic ecosystems using artificial neural networks. – *Sci. Total Environ.* 327: 105–122.
- RIMET, F., ECTOR, L., CAUCHIE, H.M. & HOFFMANN, L. (2004): Regional distribution of diatom assemblages in the headwater streams of Luxembourg. – *Hydrobiologia* 520: 105–117.
- ROZEMA, J. (1975): The influence of salinity, inundation and temperature on the germination of some halophytes and non-halophytes. – *Acta Oecol.-Oec. Plant.* 10: 317–329.
- ROZEMA, J. & SCHAT, H. (2012): Salt tolerance of halophytes, research questions reviewed in the perspective of saline agriculture. – *Environ. Exp. Bot.* 92: 83–95.
- TIKU, B.L. (1975): Ecophysiological aspects of halophyte zonation in saline sloughs. – *Plant Soil* 43: 355–369.
- TÖRÖK, P., KAPOCSI, I. & DEÁK, B. (2012): Conservation and management of alkali grassland biodiversity in Central-Europe. – In: ZHANG, W.J. (Ed.): *Grasslands: Types, Biodiversity and Impacts*: 109–118. Nova Science Publishers Inc., New York.
- TÖRÖK, P., VALKÓ, O., DEÁK, B., KELEMEN, A. & TÓTHMÉRÉSZ, B. (2014): Traditional cattle grazing in a mosaic alkali landscape: Effects on grassland biodiversity along a moisture gradient. – *PLoS ONE* 9: e97095.
- TÓTH, K. & HÜSE, B. (2014): Soil seed banks in loess grasslands and their role in grassland recovery. – *Appl. Ecol. Env. Res.* 12: 537–547.
- UNGAR, I.A. (1962): Influence of salinity on seed germination in succulent halophytes. – *Ecology* 43: 763–764.
- UNGAR, I.A. (1991): Seed germination responses and the seed bank dynamics of the halophyte *Spergularia marina* (L.) Griseb. – In: SEN, D.N. & MOHAMMED, S. (Eds.): *Marvels of seeds*: 81–86. Univ. Jodhpur, India.
- VALKÓ, O., TÓTHMÉRÉSZ, B., KELEMEN, A., SIMON, E., MIGLÉCZ, T., LUKÁCS, B.A. & TÖRÖK, P. (2014): Environmental factors driving vegetation and seed bank diversity in alkali grasslands. – *Agri. Ecosyst. Envir.* 182: 80–87.
- VÁRBÍRÓ, G., BORICS, G. & KISS, K. (2007): Use of Kohonen Self Organizing Maps (SOM) for the characterization of benthic diatom associations of the River Danube and its tributaries. – *Arch. Hydrobiol. Supplementband Large Rivers* 161: 395–404.
- VESANTO, J. & ALHONIEMI, E. (2000): Clustering of the self-organizing map IEEE. – *Trans. Neural Netw.* 11: 586–600.
- WHITE, S.R., CARLYLE, C.N., FRASER, L.H. & CAHILL, J.F. (2012): Climate change experiments in temperate grasslands: synthesis and future directions. – *Biol. Lett.* 8: 484–487.
- WILSON, J.B., KING, W.M., SYKES, M.T. & PARTRIDGE, T.R. (1996): Vegetation zonation as related to the salt tolerance of species of brackish riverbanks. – *Canad. J. Bot.* 74: 1079–108.
- ZAR, J.H. (1999): *Biostatistical analysis*. – Prentice & Hall, New Jersey: 488 pp.
- ZLINSZKY, A., DEÁK, B., KANIA, A., SCHROIFF, A. & PFEIFER, N. (2015): Mapping Natura 2000 Habitat Conservation Status in a Pannonic Salt Steppe with Airborne Laser Scanning. – *Remote Sens.* 7: 2991–3019.

Lukács et al.: Rainfall fluctuations and vegetation patterns in alkali grasslands

Appendix E4. Cover values of the species in the four grassland types in three years (mean \pm SD). Notations: ARG – Artemisia grasslands; PUG-H – higher-elevation Puccinellia grasslands; PUG-L – lower-elevation Puccinellia grasslands; JUG – Juncus grasslands.

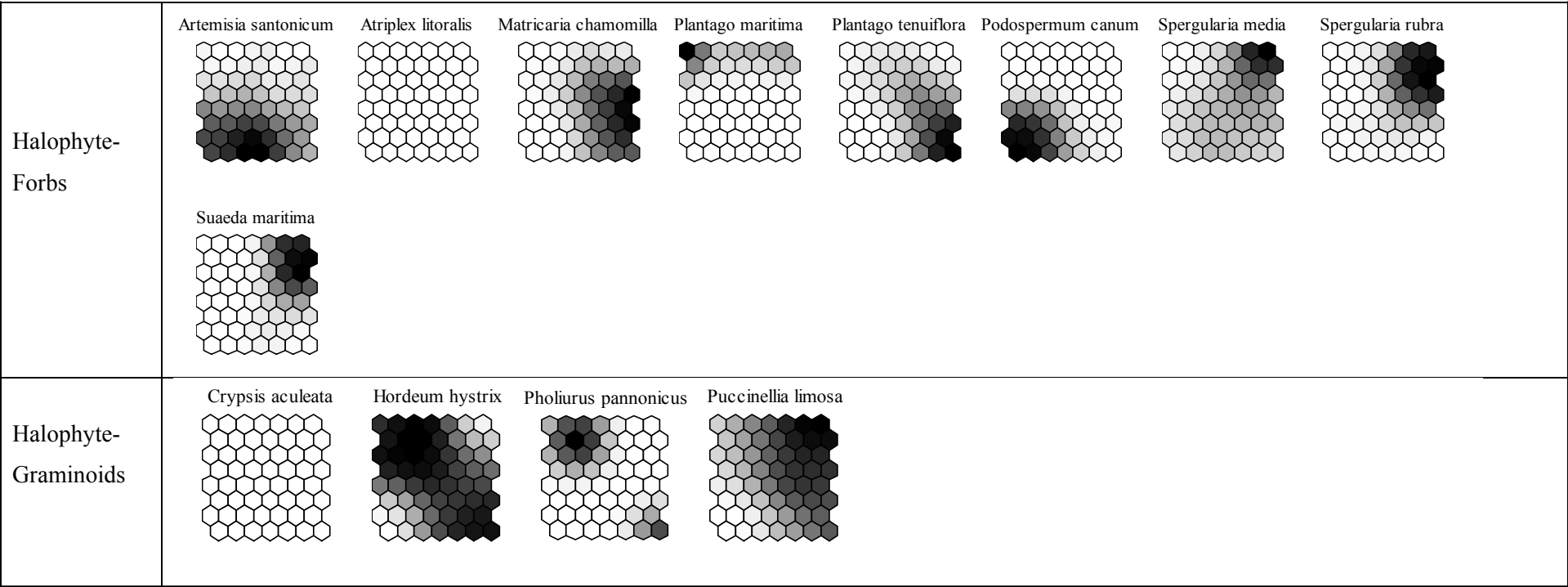
Anhang E4. Deckungsgrade der Arten in den vier Graslandtypen in den drei Jahren (Mittelwert \pm Standardabweichung). ARG – Artemisia-Rasen; PUG-H – höher gelegene Puccinellia-Rasen; PUG-L – tiefer gelegene Puccinellia-Rasen; JUG – Juncus-Rasen.

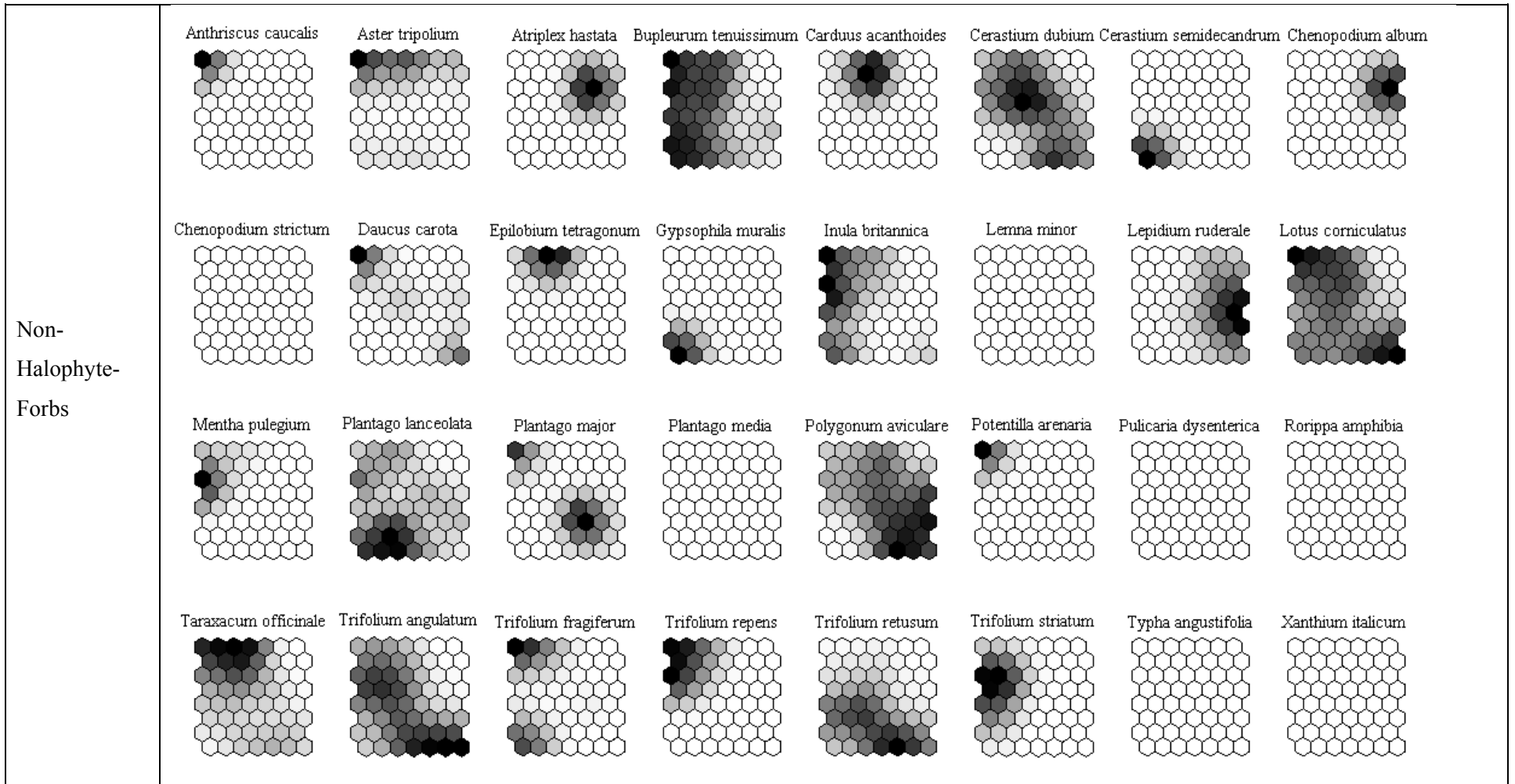
	ARG			PUG-H			PUG-L			JUG		
	2009	2010	2011	2009	2010	2011	2009	2010	2011	2009	2010	2011
<i>Agropyron repens</i>	-	-	-	-	-	-	-	-	-	0.4 \pm 0.8	-	-
<i>Agrostis stolonifera</i>	-	-	-	0.1 \pm 0.1	0.2 \pm 0.4	-	0.1 \pm 0.2	0.8 \pm 0.7	0.1 \pm 0.1	2.4 \pm 2.9	11.1 \pm 19.5	8.5 \pm 10.4
<i>Alopecurus geniculatus</i>	-	-	-	0.1 \pm 0.1	-	-	0.1 \pm 0.1	-	-	0.1 \pm 0.1	0.1 \pm 0.1	-
<i>Anthriscus caucalis</i>	-	-	-	-	-	-	-	-	-	0.1 \pm 0.1	-	-
<i>Artemisia santonicum</i>	7.1 \pm 2.4	2.0 \pm 1.0	0.9 \pm 0.8	2.1 \pm 1.7	1.5 \pm 2.0	0.8 \pm 1.6	0.7 \pm 1.0	0.1 \pm 0.1	0.1 \pm 0.1	0.5 \pm 0.7	0.1 \pm 0.1	-
<i>Aster tripolium</i> ssp. <i>pannonicum</i>	0.1 \pm 0.1	0.1 \pm 0.1	0.1 \pm 0.1	0.1 \pm 0.1	-	-	0.2 \pm 0.4	-	-	0.9 \pm 1.4	-	0.1 \pm 0.1
<i>Atriplex hastata</i>	-	-	0.1 \pm 0.1	0.1 \pm 0.1	-	0.1 \pm 0.1	-	-	0.1 \pm 0.1	-	-	0.1 \pm 0.2
<i>Atriplex litoralis</i>	-	-	-	-	-	0.1 \pm 0.1	-	-	-	-	-	-
<i>Bolboschoenus maritimus</i>	-	-	-	-	-	-	-	-	-	-	-	0.1 \pm 0.1
<i>Bromus mollis</i>	0.1 \pm 0.1	-	-	0.1 \pm 0.1	-	-	-	-	-	-	-	-
<i>Bupleurum tenuissimum</i>	0.6 \pm 0.6	0.2 \pm 0.2	0.1 \pm 0.1	0.1 \pm 0.1	0.1 \pm 0.1	0.1 \pm 0.1	0.1 \pm 0.2	-	-	0.7 \pm 0.7	-	-
<i>Carduus acanthoides</i>	-	-	-	-	-	-	0.1 \pm 0.1	-	-	-	-	-
<i>Carex acutiformis</i>	-	-	-	-	0.2 \pm 0.4	-	-	0.1 \pm 0.1	-	-	-	-
<i>Carex stenophylla</i>	4.7 \pm 4.4	3.4 \pm 1.4	3.8 \pm 6.5	1.7 \pm 3.8	1.5 \pm 2.9	0.1 \pm 0.1	-	-	-	-	-	-
<i>Cerastium dubium</i>	0.1 \pm 0.1	-	-	0.1 \pm 0.1	-	-	0.1 \pm 0.1	-	-	0.1 \pm 0.1	-	-
<i>Cerastium semidecandrum</i>	0.1 \pm 0.1	-	-	-	-	-	-	-	-	-	-	-
<i>Chenopodium album</i>	-	-	-	0.1 \pm 0.1	-	-	-	-	-	-	-	-
<i>Chenopodium strictum</i>	-	-	0.1 \pm 0.1	-	-	-	-	-	0.1 \pm 0.1	-	-	0.1 \pm 0.1
<i>Crypsis aculeatus</i>	-	-	-	-	-	-	-	-	0.7 \pm 1.4	-	-	0.1 \pm 0.1
<i>Cynodon dactylon</i>	1.9 \pm 4.2	4.0 \pm 8.8	4.1 \pm 8.8	0.1 \pm 0.1	0.1 \pm 0.1	0.1 \pm 0.1	-	-	-	-	-	-
<i>Daucus carota</i>	-	-	-	-	-	-	0.1 \pm 0.1	-	-	0.1 \pm 0.1	-	-
<i>Elocharis palustris</i>	-	-	-	-	-	-	-	-	-	-	0.1 \pm 0.1	0.6 \pm 1.3
<i>Epilobium tetragonum</i>	-	-	-	-	-	-	-	-	-	0.1 \pm 0.1	-	-
<i>Festuca pratensis</i>	-	-	-	-	-	-	-	-	-	0.1 \pm 0.1	-	-
<i>Festuca pseudovina</i>	63.3 \pm 5.8	69.6 \pm 11.2	18.5 \pm 15.7	3.2 \pm 2.4	0.7 \pm 1.0	-	0.4 \pm 0.5	-	-	1.1 \pm 1.3	-	-
<i>Gypsophila muralis</i>	0.1 \pm 0.1	-	-	-	-	-	-	-	-	-	-	0.1 \pm 0.2
<i>Hordeum hystrix</i>	3.4 \pm 2.2	1.7 \pm 1.2	12.4 \pm 5.2	18.0 \pm 13.5	7.5 \pm 12.2	3.0 \pm 4.4	17.6 \pm 12.5	26.5 \pm 21.4	0.1 \pm 0.1	36.2 \pm 10.8	1.5 \pm 1.6	0.1 \pm 0.1
<i>Hordeum jubatum</i>	-	-	-	-	-	0.1 \pm 0.1	-	0.1 \pm 0.1	-	-	-	0.1 \pm 0.1
<i>Inula britannica</i>	0.2 \pm 0.2	0.2 \pm 0.4	0.5 \pm 1	0.1 \pm 0.1	-	-	0.1 \pm 0.1	0.1 \pm 0.1	-	0.6 \pm 0.8	0.1 \pm 0.1	0.1 \pm 0.1
<i>Juncus compressus</i>	3.4 \pm 5.3	3.1 \pm 0.9	16.6 \pm 8.6	0.2 \pm 0.3	4.3 \pm 7.6	2.6 \pm 3.5	3.6 \pm 3.4	5.1 \pm 7.4	3.8 \pm 4.2	47.2 \pm 9.4	48.9 \pm 26.4	30.2 \pm 22.9

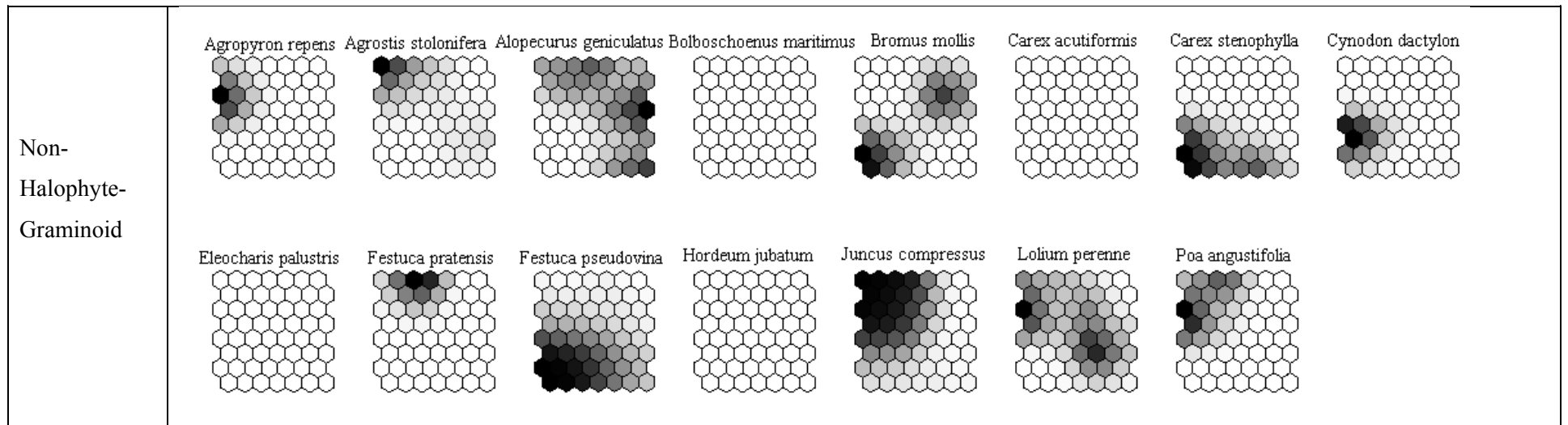
Anhang E4. Fortsetzung.[illegible]

Appendix E1. Visualisations of species distribution patterns according to the cover values in 2009. Dark colours indicate higher cover values, while light colours indicate lower values. The values are normalized between 0 and 1 to emphasise the relative importance of each group on the units of the self-organizing map (SOM). The SOM component planes correspond to the SOMs in Fig. 3.

Anhang E1. Darstellung der Verteilung der Arten entsprechend ihrer Deckungswerte im Jahr 2009. Je dunkler eine Zelle ist, desto höher liegen die Deckungswerte. Die Werte wurden 0–1-standardisiert um die relative Bedeutung jeder Gruppe auf die Einheiten der selbstorganisierenden Karten (SOM) deutlich zu machen. Die SOM-Bestandteile entsprechen den SOMs in Abb. 3.

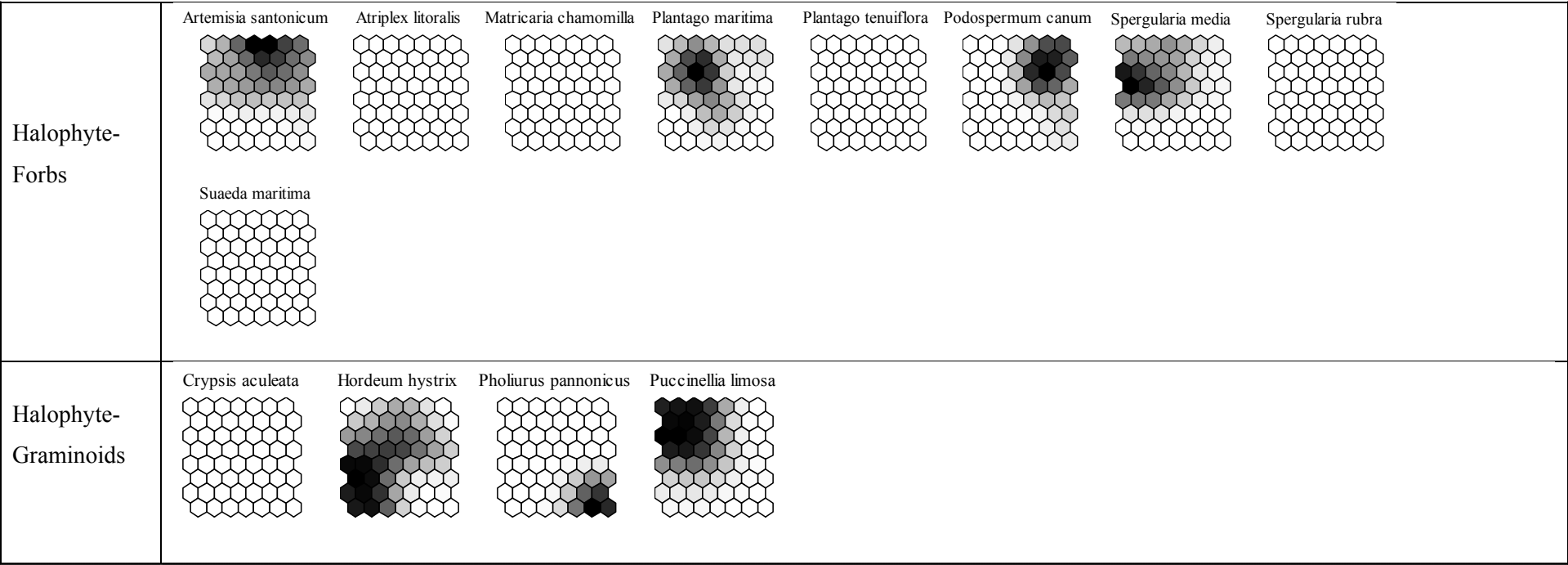




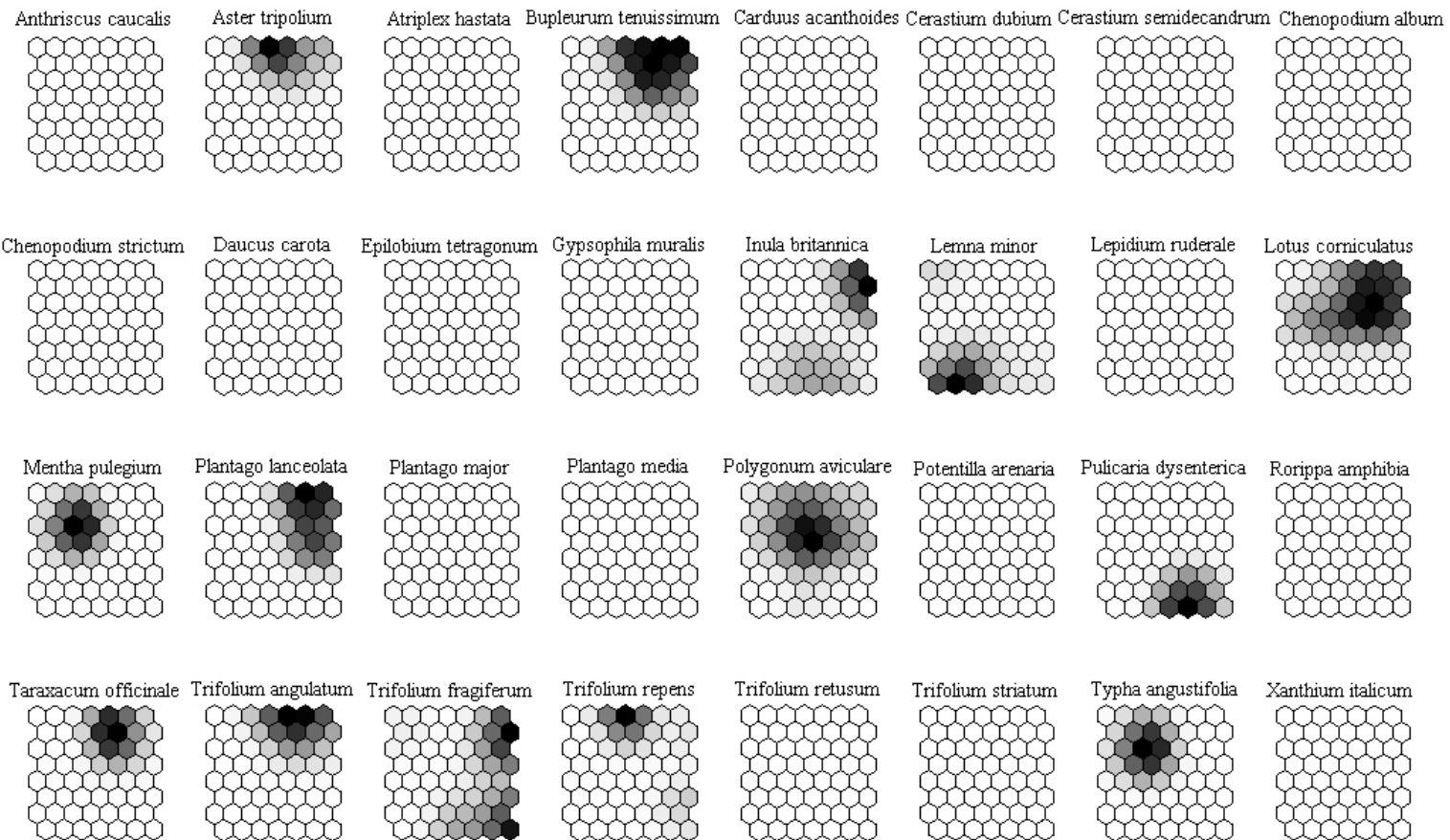


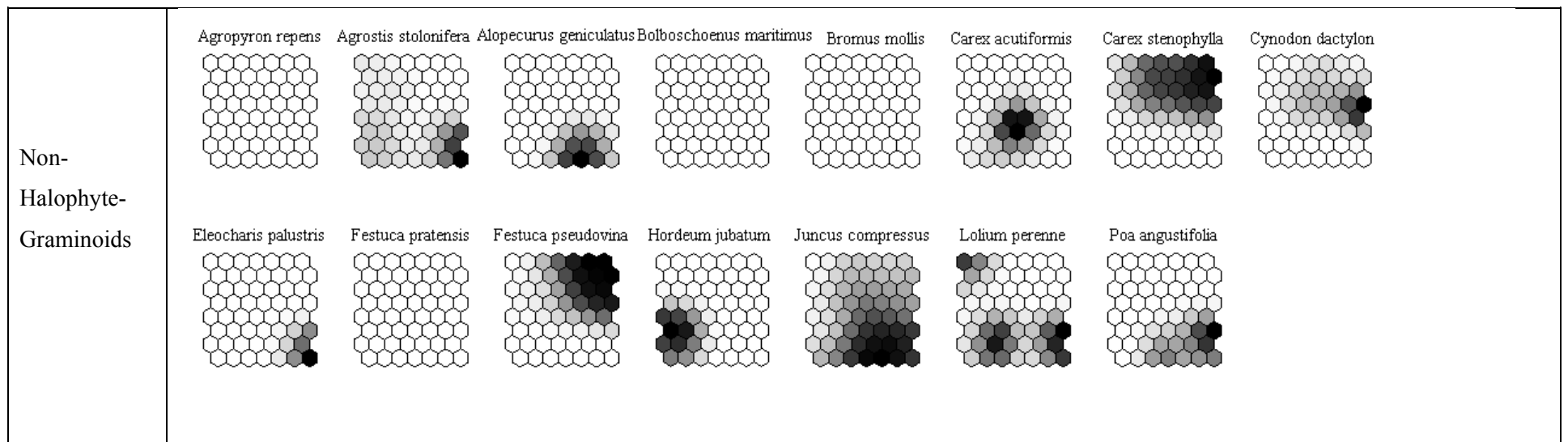
Appendix E2. Visualisations of species distribution patterns according to the cover values in 2010. Dark colours indicate higher cover values, while light colours indicate lower values. The values are normalized between 0 and 1 to emphasise the relative importance of each group on the units of the self-organizing map (SOM). The SOM component planes correspond to the SOMs in Fig. 3.

Anhang E2. Darstellung der Verteilung der Arten entsprechend ihrer Deckungswerte im Jahr 2010. Je dunkler eine Zelle ist, desto höher liegen die Deckungswerte. Die Werte wurden 0–1-standardisiert um die relative Bedeutung jeder Gruppe auf die Einheiten der selbstorganisierenden Karten (SOM) deutlich zu machen. Die SOM-Bestandteile entsprechen den SOMs in Abb. 3.



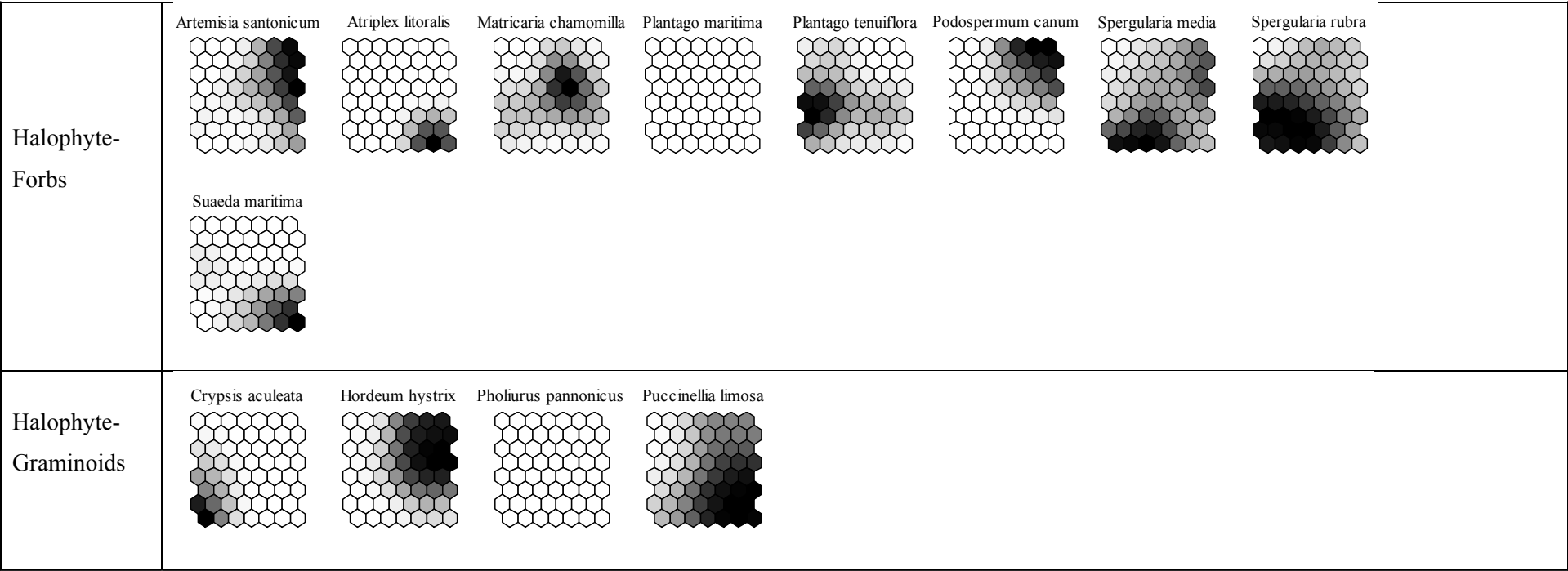
Non-
Halophyte-
Forbs





Appendix E3. Visualisations of species distribution patterns according to the cover values in 2011. Dark colours indicate higher cover values, while light colours indicate lower values. The values are normalized between 0 and 1 to emphasise the relative importance of each group on the units of the self-organizing map (SOM). The SOM component planes correspond to the SOMs in Fig. 3.

Anhang E3. Darstellung der Verteilung der Arten entsprechend ihrer Deckungswerte im Jahr 2011. Je dunkler eine Zelle ist, desto höher liegen die Deckungswerte. Die Werte wurden 0–1-standardisiert um die relative Bedeutung jeder Gruppe auf die Einheiten der selbstorganisierenden Karten (SOM) deutlich zu machen. Die SOM-Bestandteile entsprechen den SOMs in Abb. 3.



Non-
Halophyte-
Forbs

